LI.—*Notes on the Internal and External Structure of Palæozoic Crinoids.* By CHARLES WACHSMUTH*.

[Continued from p. 392.]

5. *The Construction of the Summit, and its Value in Classification.*

The construction of the ventral disk or actinal side of the calyx has heretofore received less attention than almost any other part of the Crinoids; and thereby an important aid to classification has been overlooked. I think it affords a clear and most important distinction between recent and ancient Crinoids, and shows that they fall naturally into two great divisions or groups. This view, although it does not agree with the opinion of other authors, who, in their classifications, have placed a number of Palæozoic genera in the same group with the recent Crinoids, is, as I hope to show, well founded.

Dr. F. Roemer, in the 'Lethæa Geognostica,' 1855, p. 227, divides "*the true Crinoids*, which are supported by an articulated or jointed column," into two divisions:—

a. Crinoids in which *the ventral side consists of a soft skin.*

b. Those in which *the ventral side is covered by solid immovable plates.*

Roemer includes with the former group Pentacrinidæ, Apiocrinidæ, Eugeniacrinidæ, Encrinidæ, Cupressocrinidæ, and Cyathocrinidæ. This division seems to have been based on mere conjecture, since a membranous ventral surface has been observed only in the Pentacrinidæ and the recent Crinoids generally, though it is probable that *Eugeniacrinus* and several allied genera had that summit structure. In the Apiocrinidæ and Encrinidæ, however, the general construction of the dorsal or abactinal parts, the massive plates, both of calyx and arms, indicate rather a closer relationship with the ancient Crinoids, and suggest the existence of a solid dome. The latter becomes more probable since a solid vault has been discovered in *Belemnocrinus*. This genus is in its generic formula and general form almost identical with the recent *Rhizocrinus*, which, on the contrary, is covered by a soft peristome. Both are closely related to *Apiocrinus*; *Belemnocrinus* particularly has the same heavy body-plates and the small visceral cavity; and it appears to me that *Apiocrinus* is more nearly allied to the Palæozoic type than to the recent *Rhizocrinus*.

The Cupressocrinidæ and Cyathocrinidæ are the only groups from Palæozoic formations which Roemer places in his divi-

* From 'Silliman's American Journal,' Sept. 1877.

sion *a*. Dr. Schultze, who adopted Roemer's classification, included in the Cupressocrinidæ the genera "*Synbathocrinus*, Phill., and *Phimocrinus*, L. Schl.," in which he is undoubtedly correct, for stronger reasons even than he himself perceived. These two genera agree with *Cupressocrinus* not only in the simplicity of their arms, but also in the so-called "consolidating apparatus," which he describes and figures in the latter. The apparatus is placed horizontally in *Cupressocrinus*, upright and turbinate in the two other genera. When the consolidating plates in *Synbathocrinus* are preserved, the ventral side appears to have two separate apertures, a lateral proboscis and a central mouth. And so the genus was originally described. This, however, is a misconception. By removing carefully all the arm-joints from a specimen of *Synbathocrinus*, I discovered the central aperture perfectly covered with a number of small plates; and to this summit, as it might be called, were attached narrow lateral extensions, composed of alternating pieces, which, passing downward, covered the little grooves that lead to the arm-furrows. The consolidating apparatus here forms, in fact, a part of the solid vault. It is reasonable to conclude that in the allied genera *Cupressocrinus* and *Phimocrinus*, so closely related to *Synbathocrinus* otherwise, the central opening was closed, and that the consolidating plates were further overlaid with plates forming the floor of a passage in connexion with the arm-furrows and visceral cavity. The small plates which extend out to the arms are in the specimen but partly preserved, and the connexion with the arm-furrow is interrupted; but there can be no doubt that the channel underneath contained the food-groove and ambulacral canal which I have described in *Cyathocrinus*. The covering of the central opening of *Synbathocrinus* resembles in a remarkable degree that of the central aperture of the Blastoids; and it seems to me highly probable that the consolidating plates are homologous with the partly hidden deltoid pieces of the latter.

Among the Cyathocrinidæ Roemer included genera of widely different types. Besides the typical one, he enumerates nine genera, only two of which, *Heterocrinus* and *Graphiocrinus*, have the characteristics of the Cyathocrinidæ; and both of them evidently possess a solid dome, as is proved by their heavy proboscis. All the remaining genera belong to other groups. *Macrostylocrinus* resembles *Ctenocrinus*, Bronn, and *Cytocrinus*, Roemer, so closely, that they may yet prove to be identical. Roemer, however, places *Ctenocrinus* with *Glyptocrinus* among the Crinoids with a solid dome, and *Macrostylocrinus* among the Cyathocrinidæ. *Macrostylocri-*

nus is allied to *Melocrinus*, and has undoubtedly a similar summit-structure. The same may be said of *Schizocrinus* and *Dimerocrinus*, which are not at all related to *Cyathocrinus*.

The genus *Cyathocrinus* was originally described by Prof. Phillips and Mr. Austin as having a separate mouth and vent, which was considered by these authors and others to be its chief distinction from *Poteriocrinus*. Accordingly, all species with a proboscis or solid dome, though otherwise agreeing with *Cyathocrinus*, were referred to *Poteriocrinus* or some allied genus. Meek and Worthen, however, proved (in the Geological Report of Illinois, vol. v. p. 325) that in perfect specimens the central opening is closed. The covering of *Cyathocrinus* is exceedingly interesting, and throws light upon the summit-structure of many genera. I shall herein refer frequently to Meek and Worthen's excellent figures, vol. v. pl. ix. figs. 13, 14.

Looking only at fig. 14, one would at first naturally suppose there must have been, during the life of the animal, two distinct openings in the vault. But on examining it more critically, and comparing it with fig. 13, it will be found that fig. 14 represents simply the consolidating apparatus as figured by Roemer and Schultze in *Cupressocrinus*, placed here exactly as in that genus, and consisting of five large pieces, alternating with the upper edges of the first radial plates. The plate of the anal side is larger than the others, and forms the base of the inner side of the proboscis. The five pieces, which connect with each other laterally, extend inward for some distance, but not so far as to meet in the centre, where there is a semicircular or heart-shaped opening. Along the sutures between the five plates a comparatively large furrow from each arm-base extends inward, and leads to the central opening. Examining now fig. 13 we find the general aspect of the ventral disk entirely changed. The lateral opening has been transformed into the base of a proboscis; and the consolidating plates are partly covered, leaving but a small uncovered space, in the form of a delta, in the interradial areas. The central opening is vaulted over by a number of various-sized pieces, the largest one occupying the side towards the proboscis. The shallow groove between the sutures of the consolidating plates is arched by a double series of alternating plates, forming underneath a passage for the ambulacral canal and food-groove. The vault, thus closely resembling that of *Synbathocrinus*, was in all probability arranged on a similar principle in *Cupressocrinus*. The same plan, with slight modifications, prevailed in *Poteriocrinus*,

Scaphiocrinus, and all genera with an *inflated* or *balloon-shaped ventral sac*. Among the latter the centre of radiation is frequently found to be pushed toward the anterior side, so that, owing to the great size of the sac at its junction with the dorsal cup, it does not occupy the centre of figure.

Among all groups of Crinoids, the Cyathocrinidæ undergo the least amount of change in the course of time. They are represented in the Lower Silurian by several genera; and *Cyathocrinus* is the only genus recognized in the Permian. In all intermediate formations we find Crinoids with five basals, five subradials, and five radials; and it is worthy of note that the Cyathocrinidæ, in the structure of their vault, bear closer resemblance to the recent Crinoids than almost any other group, and seem to hold an intermediate position between modern and Palæozoic types. If the alternating plates covering the furrows could be turned back at the vault by the animal as the Saumplatten of the arms, then the food-groove of these Crinoids was open throughout, as in recent forms. This might possibly have been the case in *Cyathocrinus iowensis*; but I even doubt it here, as the corresponding plates in other closely related species, though arranged upon the same fundamental plan, present rather an aspect of true vault pieces. The Cupressocrinidæ and Cyathocrinidæ thus fall naturally into a group by themselves, having the vault supported by consolidating plates, and covered by an immovable arch of small plates.

The next group, including *Taxocrinus*, *Forbesiocrinus*, *Onychocrinus*, *Ichthyocrinus*, *Lecanocrinus*, and probably other genera, is one in which, of all Palæozoic Crinoids, the vault is least known. The Taxocrinidæ (for such I will call them) have hitherto been described as being covered with some soft material instead of solid plates, even by Dr. Schultze, though he describes and figures a *Taxocrinus* with a long, heavy, plated proboscis, which could not have been supported upon a soft skin*. In this group the plates of the radial series are indented on their upper margins more or less deeply for the reception of a protuberance from the lower side of the succeeding plate. The indentation of the upper margin does not extend throughout the thickness of the plate; and in *Forbesiocrinus* it is filled by a superficial patelloid plate, which is

* I believe Dr. Schultze is mistaken in referring his *T. briareus* to *Taxocrinus*, as it lacks all the characteristic features of the genus. Its rather large subradials, the large first radials as compared with the succeeding radials, the single anal plate upon which the heavy proboscis rests, indicate that it belongs to *Cyathocrinus* or some allied genus. His *T. gracilis* may prove to be *Graphiocrinus* or *Scaphiocrinus* (?).

separately articulated and sometimes ankylosed with the outer margin of the plate above. This peculiarity not only exists in the arm-plates, but is conspicuous in the radials, thus producing apparently an articulate structure of the whole skeleton and indicating some degree of flexibility in the body as well as the arms. The interradial portions appear sometimes depressed, and in other cases swollen or bulged out, showing that they probably yielded to a moderate expansion or contraction of the body-walls, due to the mobility of the radial parts, which likewise involves a flexibility of the summit. I have not been so fortunate to find the summit of any of these genera perfectly preserved; but I feel convinced from what I have observed that it did not consist of a soft skin. In *Onychocrinus*, the genus which possessed evidently the greatest expansive power, the radial plates are frequently found spread out horizontally, and I have found towards the inner or ventral side of the radials rather large imbricating plates, to which smaller ones are attached which connect with the plates of the interradial series, and which decrease in thickness inwardly. In several specimens I found the inner part or centre of the disk covered by a number of thin, very small plates, whose arrangement could not be made out; but it is highly probable, from their size and shape, that they formed a kind of scaly integument which was pliant and flexible, thus facilitating a contraction or expansion of the dorsal portions.

The close relationship existing between *Onychocrinus*, *Forbesiocrinus*, and *Taxocrinus* renders it almost certain that their summit was similarly constructed. In *Ichthyocrinus* the peculiarities in the radial portions are less strongly marked, and the genus has no interradial plate; but as it agrees otherwise so nearly with *Taxocrinus* that it is sometimes difficult to separate them, we may feel sure that this Silurian genus forms no exception to the general rule, but that its mouth was covered as in other Palæozoic Crinoids.

That the summit in several genera has not been discovered is no proof that it consisted of soft material. During the eighteen years that I collected at Burlington I obtained several hundred of the most perfect specimens of *Cyathocrinus*, some of them as perfect in most of their parts as if dredged from the ocean; but only two specimens have been discovered in which the summit was preserved, and only a single *Scaphiocrinus*. That this could happen at a locality where even the finest tissues of the most delicate internal organs are preserved, is somewhat astonishing; but yet it can be accounted for by the fact that the pieces which cover the central opening, as also the small alternating plates forming the ambulacral canal,

are very thin, and that they rest but partly upon the consolidating plates, being thereby rendered insecure and liable to removal by any accident, even with very small force. Moreover the arms of the Cyathocrinidæ are generally attached, and the ventral disk thus hidden from view. In specimens in which the arms are destroyed their destruction almost invariably involved that of the entire ventral side; and so delicate are these parts, that even when the arms are well preserved and so situated as to expose the dome, the plates are nearly always gone, or are found in a confused mass inside the calyx.

I come now to another group, in which, on the basis of the summit-structure, such apparently diverse forms are included that I am under the necessity, very unwillingly, of making a name for it. It includes the families Actinocrinidæ, Platycrinidæ, Rhodocrinidæ, Melocrinidæ, and the genera *Schizocrinus*, *Dimerocrinus*, and *Macrostylocrinus*, which Roemer has ranged among the Cyathocrinidæ; and I call it provisionally the Sphæroidæ, from the form of the calyx, which is generally somewhat spherical. This large group, embracing over one hundred genera, and ranging from the base of the Silurian to the top of the Subcarboniferous, is capable of accurate definition, is easily distinguished, and, fortunately, the summit is very commonly found well preserved in most of the genera.

The summit is composed of heavy, frequently nodose plates, closely cemented together so as to form a *free arch* (not supported by consolidating plates), which rests like a hemisphere upon the dorsal cup. The plates of the summit, which at first sight exhibit great apparent diversity, are arranged throughout upon one and the same fundamental plan. Beginning with genera that have but few vault-pieces, we find in them the median portion occupied by one large centre plate, surrounded by six others—four large ones of equal size, and two smaller ones. The four large plates join laterally, and are often placed directly to the centre piece. In very large species and sometimes in very old specimens the plates are separated by small polygonal pieces, but easily recognized by their size. Two of the four plates lie above the interradial series adjoining the anterior ray; the two others, one at each side, are placed between the two lateral rays. The two smaller plates are separated from each other by anal plates or by the proboscis. These seven pieces, which I will call the "*apical plates*," are easily recognized by their greater prominence and size in species with comparatively few summit-plates and a lateral anal aperture; but their identification is more difficult in

species in which a subcentral proboscis is placed between the two small plates, and the whole vault looks like an immense proboscis. In these forms the four large plates, together with the two smaller ones, are pushed towards the anterior side of the specimen, while the centre plate rests with one side against the proboscis.

There are other summit-plates following a radial direction, which are either attached to the apical pieces or separated from them by a belt of small polygonal plates. Their number, which varies greatly in different species, depends upon the number of primary arms that spring out directly from the body, no matter how often the arms branch afterward. In species with only two arms to the ray, each ray has two rows of corresponding plates in the dome: one large bifurcating plate forms the upper row, three plates the second row; two of the latter are brachial plates, the third one is an interbrachial plate separating the two arms. In rays with three arms, there are eight plates in three series. The upper series consists of one large bifurcating plate, which evidently corresponds with the third radial of the dorsal side. The second series, corresponding to the secondary radials, is composed of two plates, the plate towards the division with two arms being as large as the plate of the upper series, and the one towards the single arm much smaller. The third series is formed by three brachial and two interbrachial plates. In species with four arms to the ray, both radial pieces of the second series are large, and from each of them there originate two brachial pieces. As a general rule the summit-plates increase in proportion to the number of primary arms of a species in the same manner and on the same principle as the plates of the dorsal side. Every radial from the third radial upward has a corresponding plate on the ventral side, and additional interbrachial plates between corresponding brachial plates above the arms. Therefore in adult specimens, with some little practice, the number of arms can be ascertained nearly as well from the dome as from the dorsal side. The number of vault-pieces is enormous in some genera, especially if the radials branch off alternately, as, for instance, in *Strotocrinus*, where some species have 120 to 180 arms. In looking at a full-grown specimen, with its many hundred apparently irregularly arranged vault-pieces, one would scarcely expect to be able to discover that this construction, in nearly all the Palæozoic Crinoids, is based upon a definite plan, and that plan the same as prevails below the arms. That this is the case may be successfully demonstrated in the *young Strotocrinus*, which has comparatively fewer summit-plates.

The young specimen, in genera with numerous arms, has fewer arm-openings than the adult, though both have the same number of arms. This is best observed in the young *Strotocrinus*. Here the basals, primary radials, first anal, and first interradial pieces are comparatively large, while the higher series of interradials are yet absent or but slightly developed. The radials of the higher orders, which in adult specimens form a part of the body, are in young specimens free arm plates, unsupported by any interradial or interaxillary pieces. The arms, therefore, which spring directly from the body in adult specimens, in the young branch alternately right and left after emerging from the body, the spaces between the bases of the branches being subsequently filled by the upward growth of the body, so that the branching, instead of occurring in the free arms, seems to be completed in the body-walls. So, for instance, the young *Strotocrinus umbrosus* has at first but four arm-openings to the ray; at a later period it is found to have eight, and in the adult state twelve, being a separate opening for each arm*.

The rule that the number of summit-plates increases in proportion to the number of primary arms holds good with reference to the young specimen. The young *Strotocrinus* has fewer plates than the adult individual (the difference being in proportion to the state of growth); and these are arranged in the same order, and are as easily recognized, as those of the simplest species of this group. The apical and principal radial pieces are larger than the intervening interradial plates, which, exceptionally in this genus, attain by age the same size as the apical and radial pieces. *The interradial plates* of the vault occupy the intermediate spaces between the radial areas. As their number depends greatly upon the age of the individual, they vary often in the same species. In species with but few arms, we find comparatively few interradials, and those are generally smaller than the other plates. The latter is especially true in young specimens, as also in small species. Sometimes (as, for instance, in some *Megistocrini* and all Rhodocrinidæ) the greater part of the summit is covered by large numbers of small polygonal plates which form regular belts

* A young *Strotocrinus*, unless the arms are attached, cannot be distinguished generically from an adult *Actinocrinus proboscidialis*; and as both have the same peculiar ornamentation with the same number of arm-openings, they differ but slightly in specific characters. *Actinocrinus proboscidialis* is the typical species of a small group of beautifully ornamented Crinoids, and it is evidently the forefather of all *Strotocrini*, which idea seems to be further confirmed by the geological succession. The former group occurs only in the *Lower*, and *Strotocrinus* only in the *Upper* Burlington Limestone.

around the apical and radial plates. The species of these genera, though comparatively of large size, have generally but two primary arms, and consequently for each ray but one radial dome-plate, which is here placed at some distance from the arm-bases. In the *adult Megistocrinus* the radial as well as apical plates are extremely large, and stand forth conspicuously, and each one separately, among the surrounding minute polygonal pieces. In the *young Megistocrinus*, however, and in the Rhodocrinidæ generally, the apical pieces and the radial plate are placed side by side, being surrounded by the polygonal plates. The form and size of the principal summit-plates, the distribution and number of the interradial pieces, afford most excellent characters for distinguishing many genera. In *Agaricocrinus* all apical and radial pieces are large and tuberculous, the few interradials are small. In *Dorycrinus* the centre plate and first radials are spiniferous or nodose. In *Amphoracrinus* the four large apical pieces are spiniferous or tuberculous, the radials nodose. In *Platycrinus* and *Hexacrinus* the apical plates are very prominent, often tuberculous, the radial portions are somewhat constructed like the rows of small alternating plates of the Cyathocrinidæ. In *Batocrinus* all summit-plates are nodose and almost of equal size.

The apical plates can be distinguished in other groups as well as in this. They surmount the vault of *Synbathocrinus* and *Cyathocrinus*, cover the central opening of the Blastoids, and can be traced in many of the Cystideans. This, with the further fact that they are so largely developed in young specimens, that they cover and protect some of the most important organs of the inner cavity, shows their great importance, and leads us to infer that they were the first solid parts developed on the ventral side in young Crinoids. The centre piece corresponds evidently with the basals of the dorsal side, the surrounding plates to the subradials (the two smaller plates separated by the anus forming together one large one), which, on the other hand, were undoubtedly the first-developed parts of the dorsal side, and the parts which are the most highly developed in the Cystideans.

The above groups, representing the three principal plans upon which the vault is constructed, embrace, according to my views, not only all those Palæozoic genera which were supposed to be covered by a membranous surface, but nearly all Palæozoic Crinoids that are known. There are some few genera, as, for instance, *Eucalyptocrinus*, with a very peculiar superstructure at the ventral side, whose affinities I have not been able to determine. There is the genus *Calceocrinus*,

which differs so widely from all other known Crinoids by its distinct bilateral symmetry and unique structure that it forms evidently a very distinct group by itself. There may be still others, differing in their summit-structure from the general plan; but I have yet to discover a single Palæozoic genus in which a special oral aperture has been identified, or in which the existence of a solid vault has been disproved or cannot be traced by analogy. Thus it may be possible that the solid vault was essential under the conditions which prevailed in the earlier geological ages.

Closely related as the recent Crinoids are to their Palæozoic ancestors in some points, the solid vault of the latter cannot in the remotest degree be homologized with the soft peristome of the former. The solid dome forms, as I think I have proved, a continuation of the radial and interradial series of the dorsal side, and serves merely as a covering and protection for the organs underneath. It is in every sense of the word aboral, and forms a part of the abactinal system, which, being already reduced in the Pentacrinidæ and Comatulidæ to a narrow tentacle-furrow, recedes in the Palæozoic Crinoids one step further, and disappears within the solid walls of the body. The actinal system here consists externally only of the arm-furrows, whence it continues underneath the vault. These Crinoids, therefore, are evidently of lower development and belong to an inferior type.

The ventral peristome of the recent Crinoids serves as a madreporic apparatus, introducing the necessary water for respiration. It is capable of expansion, and does expand when water or food is introduced into the inner cavity, and contracts when refuse matter is expelled. These are functions which the solid vault could not have performed; and there must have been, consequently, important modifications in the internal economy of these animals. Comparing the large size of the calyx of the *earlier* Crinoids with the small cup and large long arms of the *recent* types, we find in the former an approach to the *Cystideans*, as also a striking resemblance to the nascent *Pentacrinus* before its arms are fully developed. In the older forms, the radial plan is almost overshadowed by the bilateral arrangement of the vault, which reminds of the bilateral symmetry in the earlier stages of other Echinoderms. All these facts tend to prove that the *Palæozoic Crinoids*, embracing therein all *true Crinoids in which the actinal side is closed*, represent the young stage of growth of the living types. They bear evidently the same relation to the Pentacrinidæ and Comatulidæ as the Perischoechinidæ *bear to the* Echini, *as the Cystideæ and Blastoideæ bear to the Palæozoic*

Crinoids. They unquestionably form a *distinct group* of Crinoids; and I therefore propose for it, from the fact that its representatives lived almost exclusively in Palæozoic times, the name "*Palæocrinoidea*," *as a suborder of the Crinoids.*

Whether *Encrinus*, *Apiocrinus*, and allied genera of the Jurassic time are to be brought within this suborder, depends upon the construction of their vault, which cannot at present be determined. Should they prove to have a solid dome, they would be included here; and this might detract slightly from the technical exactness of the name *Palæocrinoidea.* Still, as its characteristic types were so prevalent, and constituted so important a part of the life of Palæozoic ages, and the Mesozoic forms are comparatively so insignificant in variety and abundance, the term would nevertheless be significant and appropriate.

I shall not attempt to separate the Palæocrinoidea into families, as I think our present knowledge is hardly sufficient for such a work; but I feel convinced that it must be based mainly upon the diversities in the structure of the vault, not upon the construction of the dorsal cup, nor upon the structure of the arms or column, upon which former authors have founded such divisions.

The discoveries which have been made within the last few years, both in recent and extinct Crinoids, are really wonderful, and lead us to expect large additions to our knowledge in the future. I observe, in the February number of the 'American Journal,' that Prof. Thomson has discovered at great depth two new genera of Apiocrinidæ, one of them resembling in superficial structure the genus *Poteriocrinus.* This may throw new light upon the physiology of the extinct types and solve some of the questions herein suggested. Other discoveries will follow. The labours of the zoologist will supplement the researches of the palæontologist; and through their properly united efforts we may hope in time to comprehend the structure of the Palæocrinoidea almost as perfectly as if they were yet living in our oceans.

LII.—*Description of a remarkable new Form of* Ophiuridæ *from Ceylon.* By Edgar A. Smith, F.Z.S.

The specimen about to be described was presented to the British Museum in 1875 by Mr. E. W. H. Holdsworth, by whom it was collected at Ceylon.

Apparently it is closely related to the genus *Ophiothela* of